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ABSTRACT

Groupers have historically been an important component of the Bermuda fishery. The coney (*Cephalopholis fulva*) comprised almost 50% of the total landed weight of all grouper species in Bermuda from 1991 – 2003. In light of this significant contribution to fishery landings and because little is known about the fishery biology of the coney, a study was initiated in January 2000.

One of the principal components of this study was to examine age and growth. Opaque rings on polished transverse sections of sagittal otoliths were used to estimate age. Fish were collected by hook and line from several locations on the Bermuda reef platform. Fork lengths of conies sampled ranged from 151 mm to 384 mm. Age estimates, determined for 997 specimens, ranged from 2 to 28 years with wide variability in the length-at-age. There was a significant positive correlation between otolith weight (OW) and age estimates which will enable the use of OW as a proxy for age of conies in future stock assessments.

The other important aspect of the study was to characterize the sexual pattern and reproductive biology of the coney. Gonads were examined histologically to confirm sex and reproductive condition. The results confirm protogynous hermaphroditism in this species. Of the 998 fish sexed, 46.1% were female, 40.1% were male and 13.8% were transitional fish. There was considerable overlap in the length distributions of males (mean length 256 mm FL \pm 28 mm SD), females (mean length 232 mm FL \pm 34 mm SD) and transitionals (mean length 241 mm FL \pm 30 mm SD) and the overall sex ratio was female biased (1.15F:1M). The reproductive season was from April to July inclusive with peak spawning occurring in June.

KEY WORDS: Coney, *Cephalopholis fulva*, age, growth, reproduction, Bermuda

Edad, Crecimiento y Reproducción de la Cherna Cabrilla (*Cephalopholis fulva*) en Bermuda

Históricamente las chernas han constituido un componente importante en la pesquería de Bermuda. La cherna cabrilla (*Cephalopholis fulva*) agrupa prácticamente el 50% del total del peso efectivo en muelle de todas las especies de chernas, desde el año 1991 – 2003. A la luz de esta importante contribución a los desembarques pesqueros, y debido a que se conoce muy poco acerca de la biología pesquera de la cherna cabrilla, se inició un estudio

en Enero de 2000.

Uno de los componentes principales de este estudio lo constituyó el examen de la edad y el crecimiento. Los anillos opacos en las secciones transversales pulidas del otolito sagital se utilizaron para estimar la edad. Los peces se capturaron con anzuelo y cordel en diferentes localidades de la plataforma del arrecife de Bermuda. Alrededor de 1000 chernas cabrilla fueron muestreadas con longitudes de bifurcaciones que fluctuaron entre 154 mm y 384 mm. Los estimados de edad fluctuaron entre los 2 y 28 años con gran variabilidad de talla con relación a la edad. Hubo una importante correlación positiva entre el peso del otolito y los estimados de edad lo cual permitió la utilización del peso del otolito como un representante para la edad de las chernas cabrilla en futuras evaluaciones del stock.

Otro aspecto importante del estudio fue la caracterización de los patrones sexuales y la biología reproductiva de la cherna cabrilla. Se examinaron las gónadas microscópicamente para confirmar el sexo e identificar los peces de transición. Los resultados confirman el hermafroditismo protógino en esta especie. De los 998 peces examinados, el 46.1 % perteneció a las hembras, el 40.1 % a los machos y el 13.8 % fueron peces de transición. Hubo un considerable solapamiento en las distribuciones de longitud de los machos (la longitud promedio fue de 255 mm FL \pm 28 mm SD), hembras (la longitud promedio fue de 232 mm FL \pm 34 mm SD), y los de transición (la longitud promedio fue de 240 mm FL \pm 28 mm SD) y el coeficiente de sexo global fue sesgado por las hembras (1.15F:1M). La temporada reproductiva fue desde abril a julio con un pico de desove en el mes de junio.

PALABRAS CLAVES: Cherna cabrilla, *Cephalopholis fulva*, edad, crecimiento, reproducción, Bermuda

INTRODUCTION

Epinepheline groupers are an important and valuable fishery resource and have historically dominated the Bermuda fishery and the fisheries of many Caribbean countries, Florida, the Gulf of Mexico and southeastern United States. However, due primarily to intense fishing pressure, the stocks of many large groupers have drastically declined (Sadovy 1994, Luckhurst 1996). At Bermuda several large grouper species such as the Nassau grouper (*Epinephelus striatus*) and the yellowfin grouper (*Mycteroperca venenosa*) have become commercially extinct.

With the decline of large grouper landings in Bermuda from 1975-1981 and a subsequent fishpot ban in 1990, there was a substantial increase in the landings of small groupers such as the coney (*Cephalopholis fulva*) and the Creole fish (*Paranthias furcifer*) because, in part, due to their ability to be readily taken by hook-and-line fishing (Luckhurst 1996). Fisheries statistics collected from local fishermen show that from 1991 to 2003, the coney alone comprised almost 50% of the total landed weight of groupers.

Relatively little is known about the biology of this species and before the present study, there had been limited research conducted on *C. fulva* at

Bermuda. A greater understanding of the fishery biology of the coney is essential in order to assess the stock around Bermuda and to make informed fishery management decisions.

MATERIALS AND METHODS

Cephalopholis fulva samples for this study were collected monthly in 2000 and 2001 by hook-and-line fishing from several locations on the Bermuda reef platform. Specimens collected from opportunistic sampling ($n = 109$) conducted in 1998 and 1999 were also included in analyses. The majority of the sampling was conducted on board the Bermuda Government research vessel *R/V Calamus* with the aid of several Fisheries staff. Samples were taken in water depths ranging from 11 to 42 metres. Captured specimens were immediately placed on ice and later brought back to the laboratory and weighed to the nearest 0.1 g. Fork length (FL), which is essentially equal to total length (TL) in coney due to the convex caudal fin shape, and standard length (SL) were measured to the nearest 1 mm. Occasionally, due to time constraints, specimens were frozen and processed at a later date.

Age and Growth

Sagittal otoliths were removed from specimens using forceps after a vertical cut was made with a large knife through the skull just anterior to the pre-opercle. The otoliths were then washed thoroughly in fresh water, dried and stored in vials until processing. Individual otoliths were weighed to the nearest 0.0001 g.

There was no significant difference between the weights of the left and right otoliths so the left otolith was chosen for analysis. Otoliths were processed following the methods of Secor et al. (1991). They were embedded in Araldite epoxy resin and left to harden for at least 24 hours. A 2- to 3-mm transverse section, that included the otolith core, was cut using an Isomet, low-speed, diamond blade saw and secured to a microscope slide by Crystal Bond adhesive. Otolith sections were then hand polished in order to clearly define presumed annuli. Presumed annuli were counted by two independent readers for a subset of otoliths ($n = 275$) using a compound microscope and then compared. If there were any discrepancies in age for any reading, that otolith was read again independently. If there was still no agreement, an age for the otolith was reached through discussion and consensus. The remaining otoliths were read by one reader.

Attempts were made to validate presumed annuli by chemically marking the otoliths. Fish held for age validation were caught by hook-and-line in September 2000. Following capture, a total of 15 fish were fresh water dipped for four minutes to rid them of ectoparasites, and following which they were tagged with Floy T-bar anchor tags inserted into the musculature below the dorsal fin rays on the left side. They were then injected with Promycin (oxytetracycline hydrochloride - OTC) in the abdominal area at an approximate dosage of 0.1 cm^3 per 100 g of wet body weight. All fish were put in a 1,000 L open water tank system with natural temperature fluctuations and fed on a diet of squid and anchovies. Most fish died by December 2000 but four fish

survived for seven months. Otoliths from these fish were examined under the microscope using ultra-violet light to detect the OTC mark in order to determine post-injection growth.

The von Bertalanffy growth parameters were estimated from observed length-at-age data by non-linear regression analysis fitting the von Bertalanffy growth model ($L(t) = L_{\infty} * [1 - \exp\{-K * (t - t_0)\}]$). Data from one locality on the Bermuda platform (n = 330) were excluded from this analysis due to unexplained abnormally high variability of length-at-age of coney at this location.

Sexual Pattern and Reproductive Seasonality

The sex of *C. fulva* during non-spawning periods was difficult to ascertain macroscopically, therefore, all sex determinations were made by microscopic examination. Gonads were removed, weighed to the nearest 0.01g and preserved in Davidson's solution for a minimum of 48 hours. They were then transferred to 50% ethanol for a minimum of 48 hours and subsequently stored in 70% ethanol in preparation for histological processing at a later date (Hinton 1990).

The posterior portion of the gonad was used for histological analysis. Preserved tissues were embedded in paraffin, cut in cross-section at 7 μ m, stained with double-strength Gill hematoxylin, and counterstained with eosin-y. Processed sections were examined microscopically by two independent readers, and there was general agreement on the interpretation of the gonad structure.

Sex and sexual maturity were determined by adapting the histological criteria of sexual development of McGovern et al (1998) (Table 1). Sexual pattern was assessed using the criteria outlined in Sadovy and Shapiro (1987).

Coney fork length data was not normally distributed so lengths of males, females and transitionals were compared by an ANOVA on log-transformed data. Chi-square tests were used to determine if observed sex ratios differed significantly from a 1:1 ratio.

Only mature females, for which reproductive stage was certain, were used to determine reproductive seasonality in coney. Females with hydrated oocytes or postovulatory follicles were considered to be in spawning condition. Mean gonadosomatic index (GSI) was used to assess relative changes in reproductive state during the year. The GSI index was calculated using the formula:

$$\text{GSI} = [\text{GW}/(\text{TW}-\text{GW})] \times 100$$

where GW = gonad weight and TW = total wet weight.

The temperature of the water just above the reef substrate was recorded using a Stowaway Waterproof Temperature Logger. This environmental variable may be important to some groupers in determining time of spawning (Colin 1992).

Table 1. Histological criteria used to determine sex and reproductive stage in coney (adapted from McGovern et. al,1998).

Reproductive stages	Histological Criteria	
	Females	Males
Immature	Previtellogenic oocytes; no evidence of atresia; differentiated from resting females by lack of muscle and connective tissue bundles in lamellae, oogonia more abundant along periphery of lamellae, thinner ovarian wall, smaller ovarian transverse section and shorter lamellae.	Possible primary males. Immature males as described by Moe (1969) were considered late transitionals as sexual transition not yet complete.
Mature, resting	Previtellogenic oocytes; traces of atresia; differentiated from immature females by presence of muscle and connective tissue bundles in lamellae, oogonia less abundant along periphery of lamellae, thicker ovarian wall, larger ovarian transverse section and more elongated lamellae.	Empty lobules and sinuses with little or no spermatocyte development.
Developing	Oocytes undergoing cortical aveoli formation through late vitellogenesis (migratory nucleus and partial coalescence of yolk globules).	Spermatogenesis occurring; cysts of primary and secondary spermatocytes through some accumulation of spermatozoa in lobules and peripheral sinuses within the gonadal wall.
Developing, recent spent	Developing stage as described above with the addition of postovulatory follicles.	
Running ripe	Coalescence of yolk globules complete; presence of hydrated oocytes.	Predominance of spermatozoa in lobules and peripheral sinuses with little or no spermatogenesis occurring.
Spent	More than 50% of the vitellogenic oocytes in alpha or beta stages of atresia.	Some residual spermatozoa in lobules and peripheral sinuses with no spermatogenesis occurring.
Transitional	Proliferation of testicular tissue (spermatogonia through limited spermatogenesis) within lamellae of spent or resting ovary; development of peripheral sinuses in musculature of ovarian wall.	

RESULTS

Age and Growth

Age estimations were determined for 997 specimens. All otoliths exhibited an alternating pattern of opaque rings and translucent zones. Opaque rings were counted as presumed annuli (Figure 1). Attempts to validate rings as annuli met with limited success. Out of the four specimens that survived seven months of the age-validation experiment, OTC marks were only visible in two specimens. Some growth was observed distal to the OTC mark and the last presumed annulus on these specimens. This observation tends to support the hypothesis that rings are deposited annually but is not a validation.

Estimated coney ages ranged from 2 to 28 years and sizes ranged from 151 mm to 384 mm FL. The oldest specimens were male with ages ranging from 4 to 28 years. Female ages ranged from 2 to 22 years but the majority (97%) were between the ages of 2 and 12 years. Transitionals (see sexual pattern section) ranged from 4 to 23 years of age with the majority (94%) between the ages of 4 and 12 years (Figure 2).

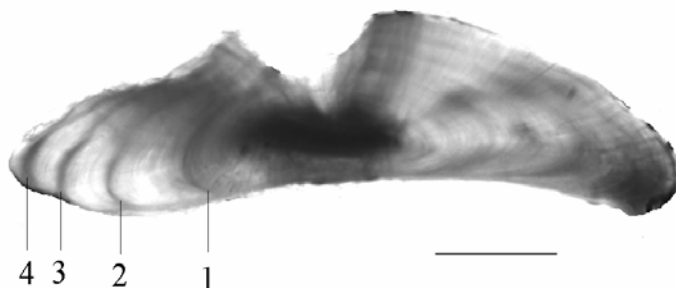


Figure 1. Transverse sagittal otolith section of a coney, 198 mm FL, estimated to be four years old. Scale bar = 0.5 mm.

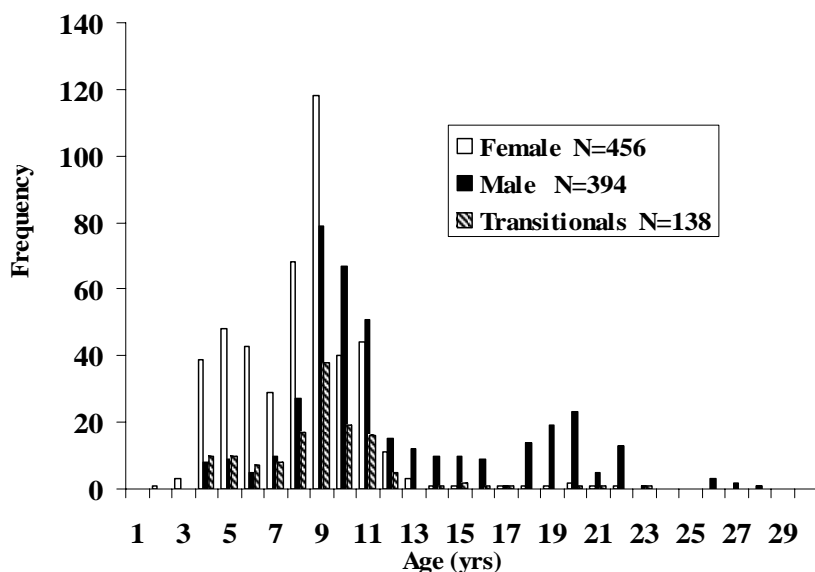


Figure 2. Age distribution of male, female and transitional coney at Bermuda

There was wide variability in the length-at-age of the fish sampled (Figure 3) thus length was not a good predictor of age. The length of the oldest fish sampled (28 years) was 295 mm FL, while the largest fish sampled (384 mm FL) was only eight years old.

Although there was not a good correlation between length and age, there was a positive correlation between otolith weight and age ($r^2 = 0.73$; Figure 4). This relationship will allow for the use of otolith weight as a proxy for age in future stock assessments such as suggested for lane snapper (*Lutjanus synagris*) (Luckhurst et al. 2000).

The equation that best describes this relationship for coney is:

$$OW = 0.0025 * \text{age} + 0.00161$$

The equation that shows the relationship between total body weight (W) and fork length (FL) is:

$$W = 0.000011 * FL^{3.0749} (N = 982, r^2 = 0.9622)$$

The von Bertalanffy growth parameter estimates obtained from observed lengths at age were as follows:

$$L_{\infty} = 280.86 \pm 3.5862 \text{ SE}$$

$$K = 0.20 \pm 0.0196 \text{ SE}$$

$$t_0 = -1.21 \text{ years} \pm 0.5922 \text{ SE}$$

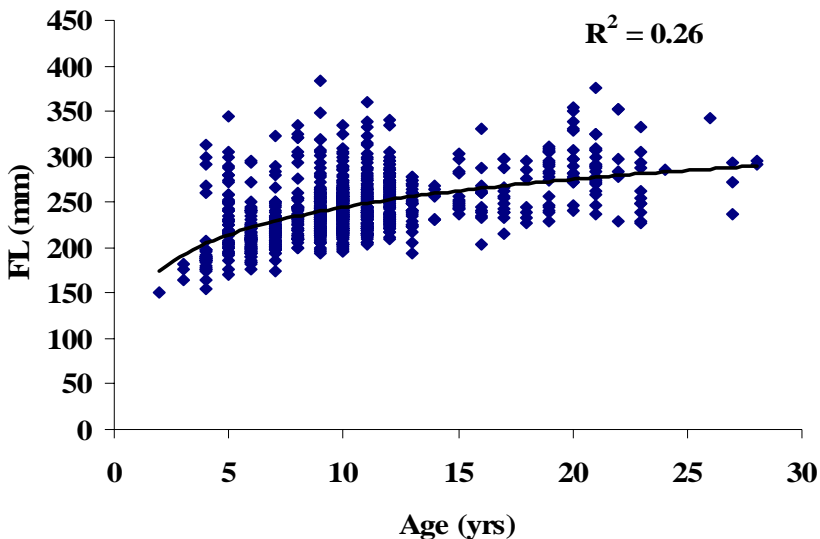


Figure 3. Fork length by age of coney at Bermuda

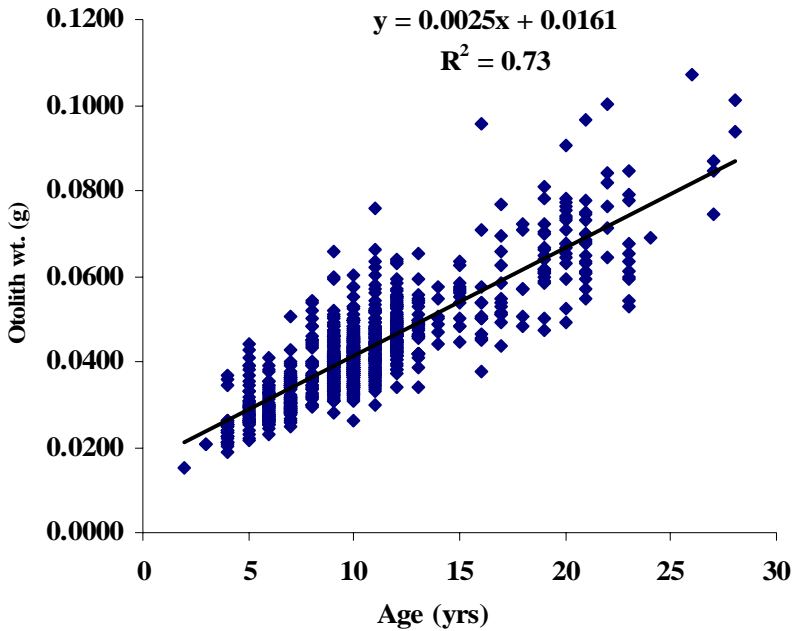


Figure 4. Otolith weight vs. age of coney at Bermuda

Sexual Pattern and Reproductive Seasonality

Out of the 998 conies sexed, 460 (46.1%) were female and fork lengths of these specimens ranged from 151 mm to 384 mm. A total of 400 fish (40.1%) were male with fork lengths of specimens ranging from 190 mm to 353 mm. Transitionals accounted for 13.8% (138 individuals) of the total sexed fish (Figure 5). Fork lengths of transitional specimens ranged from 194 mm to 375 mm.

There was considerable overlap in the length distributions of males, females and transitionals and the mean lengths between the sexes were significantly different (ANOVA, $F = 70.06$, $p < 0.001$). The mean length of males was 256 mm FL (± 28 mm SD). Female mean length was 232 mm FL (± 34 mm SD) and mean length of transitionals was 241 mm FL (± 30 mm SD) (Figure 6).

The overall sex ratio was slightly female biased (1.15F:1M, $n = 860$, $\chi^2 = 4.19$, $P = 0.04$). During the non-reproductive months the female bias was much greater (1.75F:1M, $N=478$, $\chi^2 = 35.36$, $P < 0.0001$), however, during the reproductive season (April - July), males significantly outnumbered females (0.69F:1M), $N=382$, $\chi^2 = 12.83$, $p = 0.0003$).

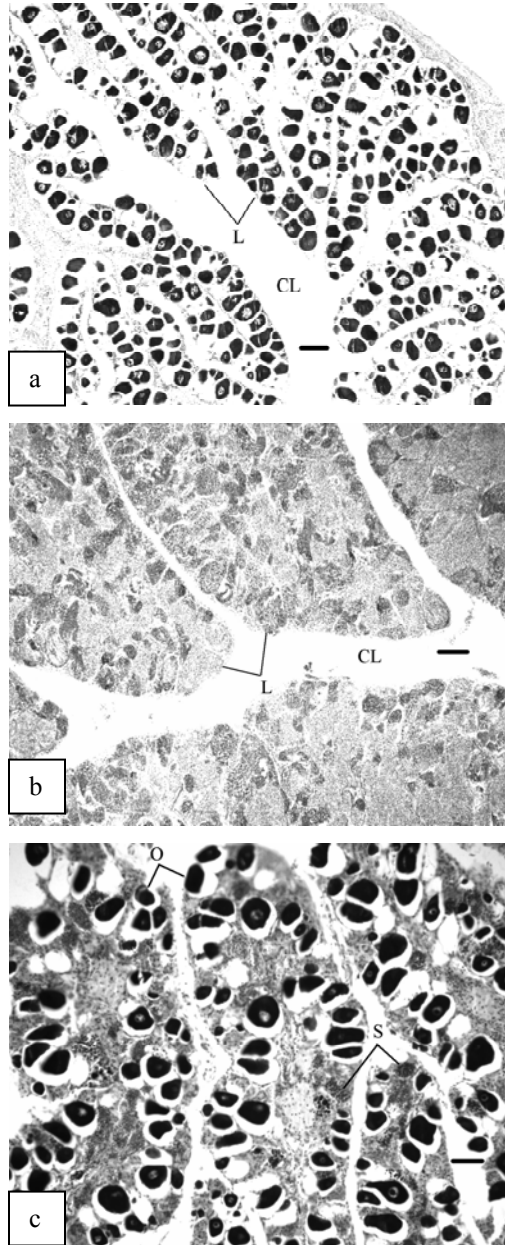


Figure 5. Cross-sections of gonads of *C. fulva* (a) Ovary with central lumen and lamellae of female, 235 mm FL (b) Testis with central lumen and lamellar structure of male, 274 mm FL and (c) Transitional gonad of individual, 252 mm FL. Symbol key: L = lamellae; CL = central lumen; O = oocyte (ovarian tissue); S=cysts of spermatogenic cells (testicular tissue). Scale bar = for (a) & (b), 100 μ m; for (c) 50 μ m.

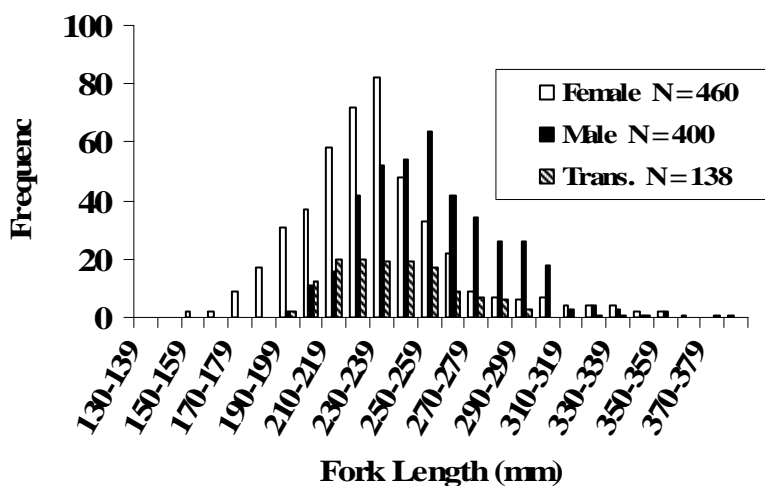


Figure 6. Length frequency distribution of male, female and transitional coney at Bermuda.

Female and male conies followed a similar pattern of sexual activity. Gonadal development occurred as early as February (Figure 7) but most reproductive activity commenced in April. Peak spawning occurred in June. Many males were still in spawning condition in July although only one spawning female was caught during this month. By August most fish were in a resting stage and from August until March, there was little reproductive activity. Many resting females were also recorded from July and spent fish were noted during the whole reproductive season. Transitional fish were found during all months of the year.

The GSI plot confirms the summer spawning season with the highest GSI values occurring in June (Figure 8). The mean monthly water temperature during the sampling period ranged from a low of 18.9°C in March to a high of 28.2°C in August. Spawning appeared to occur at temperatures between 22°C - 26°C.

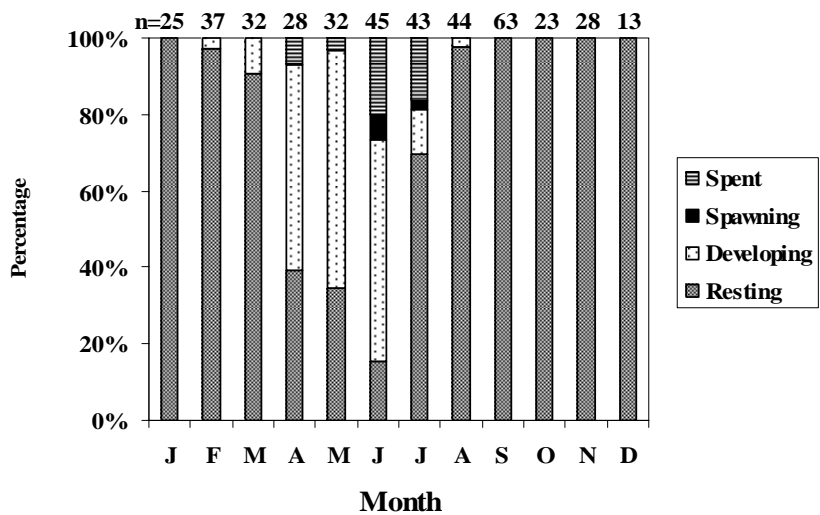


Figure 7. Percentage composition of female coney reproductive stage by month (n = 413)

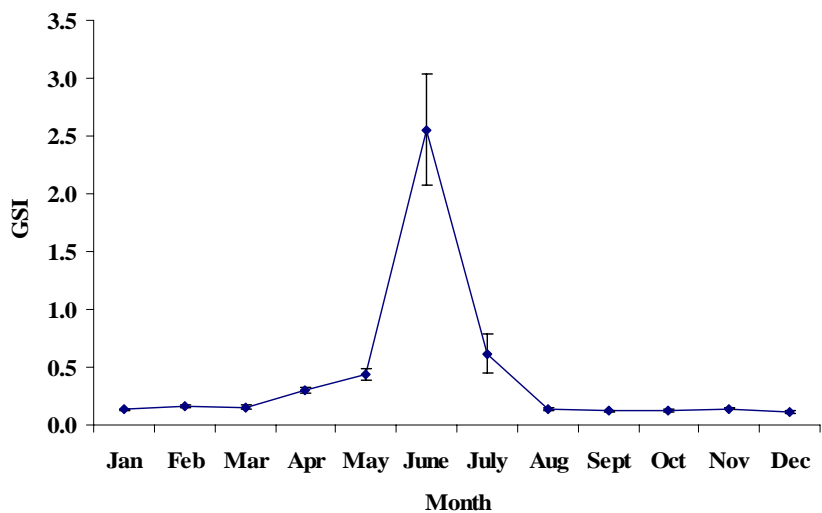


Figure 8. Mean gonadosomatic index (GSI) plot (\pm SE) of female coney at Bermuda

DISCUSSION

Age and Growth

The maximum age of 28 years observed in coney at Bermuda is much older than previously indicated for this species. Potts and Manooch (1999) observed a maximum age of only 11 years for coney from the Southeastern United States with reported size ranges that were similar to those from Bermuda (150 mm to 397 mm TL).

Estimates of L_{∞} and K for coney at Bermuda were also much lower than those estimated by Potts and Manooch ($L_{\infty} = 372$ and $K = 0.32$) for coney from the Southeastern United States and those estimated by Thompson and Munro (1978) for coney from Jamaica ($L_{\infty} = 340$ and $K = 0.63$). This would suggest that coney at Bermuda attain a smaller asymptotic size and are much slower growing than coney in the USA and Caribbean. It must be noted that the sample size from the present study was substantially larger than that of Potts and Manooch's sample ($n = 55$) and thus would have better captured the natural variability of growth in coney.

Although age estimates are preliminary in this study, it is felt that they are reasonable due to the high legibility of the otoliths, the occurrence of other long lived fish species at Bermuda (Luckhurst 2000, unpublished data) and the validation of annuli by OTC markings in a similar grouper, the red hind, *Epinephelus guttatus*, at Bermuda (Luckhurst Pers. comm.).

Sexual Pattern and Reproductive Seasonality

The presence of transitional individuals, testes that retained an ovarian lumen and lamellar structure and sperm sinuses in the gonadal wall confirmed previous indications of protogynous hermaphroditism in *C. fulva* (Sadovy and Shapiro 1987, Smith 1959, Smith 1965). Transitionals showed wide variability in the proportion and stages of development of ovarian and testicular tissue, which implied a succession from ovary to testis. Many transitionals also contained muscle and connective tissue bundles which are indicative of prior spawning as a female (Sadovy and Shapiro 1987, Shapiro et al. 1993).

The percentage of transitionals found during this study (13.8%) was very high compared to the $< 3\%$ found for many other grouper species (Shapiro et al. 1993, Bullock and Murphy 1994, Bullock et al. 1996, Brule et al. 1999, Mackie 2000, Chan and Sadovy 2002). Siau (1994), however, also found a high percentage of transitionals (10.8%) for a similar species, *Cephalopholis taeniops* (blue-spotted grouper) from the East Atlantic and Marino et. al (2001) found that 9% of *Epinephelus marginatus* (dusky grouper) from the southern Mediterranean were transitionals. Both studies, however, found that transitionals occurred primarily outside of the reproductive period. This is unlike the present study where transitionals were observed throughout the whole year. Shapiro et al. (1993) found that in red hind, *Epinephelus guttatus*, from Puerto Rico transitionals also occurred throughout the year.

Many grouper species are monandric protogynous hermaphrodites (Smith 1959, Smith 1965, Moe 1969, Thompson and Munro 1978, Shapiro 1987, Shapiro et al. 1993, Brule et al. 1999) and typically demonstrate bimodal size or age frequency distributions and female biased adult sex ratios (Sadovy and

Shapiro 1987). In some species, though, it has been discovered that males may develop directly from juveniles. This is the case with *Cephalopholis taeniops* (Siau 1994), the chocolate hind, *Cephalopholis boenak* (Chan and Sadovy 2002) and the catface rockcod, *Epinephelus andersoni* (Fennessy and Sadovy 2002). In *C. taeniops* and *E. andersoni*, mature males were observed that were smaller than mature females.

In *C. fulva* at Bermuda, there was broad overlap in fork lengths among the sexes but males were significantly larger than females. There was, however, no difference in the modal age of the sexes, which was nine years for males, females and transitionals.

While the overall sex ratio was female biased, the degree of bias was not great and was heavily influenced by a male bias observed during reproductive months. It is suspected that this male bias may have been caused by the more aggressive nature of males during spawning time in bait competition.

Diagnosis of the type of protogyny exhibited in coney was impeded by the lack of juveniles in the sample and thus the inability to detect if there was any development of males from the juvenile phase. Out of all of the specimens collected for this study, only one fish was considered to be immature (although there were many females for which maturity was uncertain). It is evident then that the size of first maturity for coney at Bermuda is below the size at which the fish recruit to the hook-and-line fishery (approx. 150 mm FL), and that examining juveniles will help to determine the sexual pattern of this species.

The summer reproductive season observed for coney in this study is consistent with previous indications for this species (Luckhurst unpublished data) and that found for other fish species at Bermuda (Bardach et al. 1958, Smith 1958, Luckhurst 1996). Thompson and Munro (1978) documented a much longer reproductive season for coney from Jamaica (November to July).

Fisheries Management

Presently there are no fisheries management restrictions in place for coney at Bermuda. Although the coney has been heavily targeted for many years by both commercial and recreational fishers, it would appear from this study that the stock is still healthy. A large proportion of the sampled fish were 10+ years. The presence of these older year classes suggests that fishing mortality is not yet high enough to remove these individuals from the population.

The fact that the majority of the fish sampled during this study were mature fish may lend some insights into the continued abundance of this species around Bermuda. It would appear that, as suggested by Chan and Sadovy (2002) for *Cephalopholis boenak*, the small size of sexual maturation in *C. fulva* at Bermuda makes it less susceptible to fishing pressure. This is because these fish have an opportunity to reproduce before being captured by the line fishery. Before the fish pot ban of 1990, fish catches of coney in fish pots had increased dramatically from 1984 – 1989 (Luckhurst 1996), however, small fish may have been able to escape and thus again have a chance to spawn before being caught. Beets et. al (1994), documented a minimum length of capture of 100 mm TL for coney from the pot fishery at St. Croix, U.S. Virgin Islands. The study also indicated that total catches of this species were declining in this area and supported recommendations on increases in fish pot

mesh size so that small fish could escape and have a chance to reproduce.

Chan and Sadovy (2002) also suggest another reason why small grouper species such as the coney have been able, in some cases, to remain abundant. They reason that with the overfishing of larger groupers, predation and interspecific competition would have been reduced, thus allowing smaller species to flourish.

While it does not appear that coney at Bermuda require any specific management action at this time, the present study will provide the basis for monitoring and assessing the status of the population into the future.

LITERATURE CITED

- Bardach, J.E., C.L. Smith, and D.W. Menzel. 1958. Bermuda fisheries research program final report, Bermuda Trade Development Board, Hamilton, Bermuda. 59 pp.
- Beets, J., A. Friedlander, and W. Tobias. 1994. Stock analysis of coney in the U.S. Virgin Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute* **43**:403-416.
- Brule, T., C. Deniel, T. Colas-Marrufo, and M. Sanchez-Crespo. 1999. Red grouper reproduction in the Southern Gulf of Mexico. *Transactions of the American Fisheries Society* **128**:385-402.
- Bullock, L.H. and M.D. Murphy. 1994. Aspects of the life history of the yellowmouth grouper, *Mycteroperca interstitialis*, in the eastern Gulf of Mexico. *Bulletin of Marine Science* **55**(1):30-45.
- Bullock, L.H., M.F. Godcharles, and R.E. Crabtree. 1996. Reproduction of yellowedge grouper, *Epinephelus flavolimbatus*, from the eastern Gulf of Mexico. *Bulletin of Marine Science* **59**(1):216-224.
- Chan, T.T.C. and Y. Sadovy. 2002. Reproductive biology, age and growth in the chocolate hind, *Cephalopholis boenak* (Bloch, 1790), in Hong Kong. *Marine and Freshwater Research* **53**:791-803.
- Colin, P.L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes* **34**:357-377.
- Fennessy, S.T. and Y. Sadovy. 2002. Reproductive biology of a diandric protogynous hermaphrodite, the serranid *Epinephelus andersoni*. *Marine and Freshwater Research* **53**:147-158.
- Hinton, D.E. 1990. Histological techniques. Pages 191-211 in: C.B. Schreck and P.B. Moyle (eds.). *Methods for Fish Biology*. American Fisheries Society, Bethesda, Maryland USA. 684 pp.
- Luckhurst, B.E. 1996. Trends in commercial fishery landings of groupers and snappers in Bermuda from 1975 to 1992 and associated fishery management issues. Pages 286-297 in: F. Arreguin-Sanchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.). *Biology, Fisheries and Culture of Tropical Groupers and Snappers*. ICLARM Conference Proceedings No. 48. 449 pp.
- Luckhurst, B.E., J.M. Dean, and M. Reichert. 2000. Age, growth and reproduction of the lane snapper *Lutjanus synagris* (Pisces: Lutjanidae) at Bermuda. *Marine Ecology Progress Series* **203**:255-261.

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- Mackie, M. 2000. Reproductive biology of the halfmoon grouper, *Epinephelus rivulatus*, at Ningaloo Reef, Western Australia. *Environmental Biology of Fishes* **57**:363-376.
- Marino, G., E. Azzurro, A. Massari, M.G. Finoia, and A. Mandich. 2001. Reproduction in the dusky grouper from the southern Mediterranean. *Journal of Fish Biology* **58**:909-927.
- McGovern, J.C., D.M. Wyanski, O. Pashuk, C.S. Manooch III, and G.R. Sedberry. 1998. Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976-1995. *Fisheries Bulletin* **96**:797-807.
- Moe, M. 1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Florida Department of Natural Resources, Marine Research Laboratory Professional Papers Series **10**:1-95.
- Munro, J.L. and R. Thompson. 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). *Journal of Fish Biology* **12**:115-146.
- Potts, J.C. and C.S. Manooch III. 1999. Observations on the age and growth of graysby and coney from the southeastern United States. *Transactions of the American Fisheries Society* **128**(4):751-757.
- Sadovy, Y. 1994. Grouper stocks of the Western Central Atlantic: The need for management and management needs. *Proceedings of the Gulf and Caribbean Fisheries Institute* **43**:43-64.
- Sadovy, Y. and D.Y. Shapiro. 1987. Criteria for the diagnosis of hermaphroditism in fishes. *Copeia* **1987**(1):136-156.
- Secor, D., E.H. Laban, and J.M. Dean. 1991. Manual for otolith removal and preparation for microstructural examination. Technical Publication 1991-01, Belle W. Baruch Institute for Marine Biology and Coastal Research, Columbia, South Carolina USA. 85 pp.
- Shapiro, D.Y. 1987. Reproduction in groupers. Pages 295-327 in: J.J. Polovina and S. Ralston (eds) *Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Boulder, Colorado USA.
- Shapiro, D.Y., Y. Sadovy, and M.A. McGehee. 1993. Periodicity of sex change and reproduction in the red hind, *Epinephelus guttatus*, a protogynous grouper. *Bulletin of Marine Science* **53**(3):1151-1162.
- Siau, Y. 1994. Population structure, reproduction and sex change in a tropical East Atlantic grouper. *Journal of Fish Biology* **44**:205-211.
- Smith, C.L. 1959. Hermaphroditism in some serranid fishes from Bermuda. *Papers of the Michigan Academy of Science Arts and Letters* **44**:111-119.
- Smith, C.L. 1965. The patterns of sexuality and the classification of serranid fishes. *American Museum Novitates* **2077**:1-20.

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